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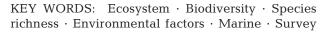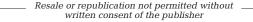
Use of fishes as sampling tools for understanding biodiversity and ecosystem functioning in the ocean

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ABSTRACT: Across the globe, regulatory bodies are moving towards an ecosystem-based approach to management (EAM) of oceans. As part of this directive, criteria have been outlined for defining ecologically and biologically significant areas and marine protected areas. One of the first steps in identifying either is the development of an inventory of species' spatial distributions and the identification of habitats used by different life history stages of these species. Many of these data have been gleaned from research vessel trawl surveys that only sample a slice of the ecosystem. Here, for the first time, food habits data collected from a trawl survey were integrated with the original trawl data to improve estimates of species richness, distribution, and habitat associations with the objective of providing additional information for an EAM. The inclusion of stomach content data increased the number and size range of species observed: its greatest value was in describing invertebrate and small finfish species richness. We found differences in the spatial patterns and the influence of environmental factors on species richness between stomach and trawl samples. We conclude that the addition of stomach data can enrich the definition process for spatial management tools, adding dimensions that would otherwise be missed. This has important implications for EAM since we may not be using all of the resources at our disposal.

KEY WORDS: Ecosystem · Biodiversity · Species richness · Environmental factors · Marine · Survey

Examples of habitats and species sampled via stomach contents of fishes captured with bottom trawls.

Photos: Fisheries and Oceans Canada (Bedford Institute of Oceanography) and Canadian Healthy Oceans Network

INTRODUCTION

Across the globe, regulatory bodies are moving towards ecosystem-based approaches to fisheries and ocean management (EAM; Garcia et al. 2003, Marasco et al. 2007, Ruckelshaus et al. 2008), which requires the integration of information on the broader ecosystem and human dimensions. National and international agreements outline the need for both sustainable use and conservation objectives to be clearly defined in an ecosystem-based approach (Shelton & Sinclair 2008). Sustainable use requires fisheries and ocean management

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plans that prevent long-term decline in stocks, species, or habitats. Conservation is required at the genetic, species, and ecosystem levels, necessitating diversity to be studied and understood not only for commercial species (target species) but also for species impacted by fisheries as incidental captures (by-catch), by second-order effects (e.g. prey removal), or species directly impacted by fishing activities (e.g. habitat disturbance).

Internationally, criteria have been established for defining 'ecologically and biologically significant areas' (EBSAs; DFO 2004, CBD 2008). Canada's Oceans Act (1996) authorizes Fisheries and Oceans Canada (DFO) to provide enhanced protection to national areas of oceans and coasts that are considered to be ecologically or biologically significant. Here, the definition of an area as 'significant' suggests that if the area were disturbed or disrupted, the ecological consequences would be greater than an equal disturbance in most other areas (DFO 2004). Significance has several dimensions and can refer to the role of habitat (benthic or pelagic), a community attribute, or the role of a species in the ecosystem.

One of the first steps in identifying EBSAs is the development of inventories of species by taxon and region, and the identification of habitats used by different life history stages of these organisms. In natural, open ecosystems, inventories of species richness are generally incomplete since it is challenging to sample the whole ecosystem, particularly in marine environments and in large ecosystems (Mikkelsen & Cracraft 2001). To date, science in large marine ecosystems has relied heavily on bottom trawl surveys for the provision of data on species and community biodiversity, abundance, and distribution. However, bottom trawl surveys only sample a slice of the species diversity contained within a marine ecosystem; they are generally designed to capture medium and large groundfish. Consequently, they do not adequately sample small fish, pelagic fish, or the multitude of small pelagic and benthic invertebrate species that inhabit marine ecosystems. To complement this information and provide data on a further suite of organisms, other sampling methods are often used (e.g. Link et al. 2002). Benthic and infaunal species are generally sampled using a benthic grab or epibenthic sled, and zooplankton are sampled with a plankton net. More recently, surveys have expanded to use photography or videography on standard survey equipment or with remotely operated submersibles to obtain inventories of all species (Moser et al. 1998, Metaxas

& Davis 2005, Stein et al. 2005). Unfortunately, combining the data from multiple sources to obtain a more synoptic view of the ecosystem is difficult, as each provides an integrated snapshot of the ecosystem at very different spatial scales and with different biases. Benthic grab samples or photographic captures, for example, measure diversity or abundance across 0.01 to 1 m^2, whereas a single standardized bottom trawl covers ~40000 m^2. Ideally, data on all levels of biota would be collected simultaneously such that all species are collected at the same scale allowing direct comparisons of different areas and habitats.

A step towards this goal is to extend the sampling capabilities of existing platforms. Using the fish retained in trawl surveys as an additional sampling tool is an obvious example. The diversity of fish species captured in trawl surveys represents a range of food habits, prey preferences, trophic levels, and feeding behaviors (Bulman et al. 2001). Essentially, fish stomachs can be considered the great integrator of their immediate biota. The diverse fish species fill the available niches in their environment and will consume many species unavailable or not retained in the trawl gear as well as some of those species that are retained (Serrano et al. 2003). Additionally, fish will feed in areas that most traditional sampling methods will not be capable of reaching such as in regions of high rugosity or on rocky substrate (Zimmermann 2003). Thus, using fish as a sampling tool should enable the sampling of a much larger slice of the ecosystem than just the sampling of fish by the trawl survey. Furthermore, the food habits data may be a cost effective and readily available information source for improving species richness estimates, as many agencies are conducting stomach content analysis as a routine part of their groundfish or 'ecosystem' surveys to provide data inputs into ecosystem models or to compare diet preferences across regions (e.g. Cook & Bundy 2010, Bundy et al. 2011). Support for the use of fish as samplers of the ecosystem is provided by Link (2004a), who extrapolated data from trawl-sampled fish stomachs to recreate abundance estimates of benthic organisms along the northeastern USA, and by Aydin et al. (2006), who used fish consumption estimates to calculate survey catchability for forage species.

Here we explored the benefits of using stomach content data (hereafter 'stomach data') from fish captured by trawl surveys from the Scotian Shelf, eastern Canada, Northwest Atlantic Ocean, as sampling tools (Fig. 1). Previous work on the Scotian Shelf has described the patterns of finfish biodiver-
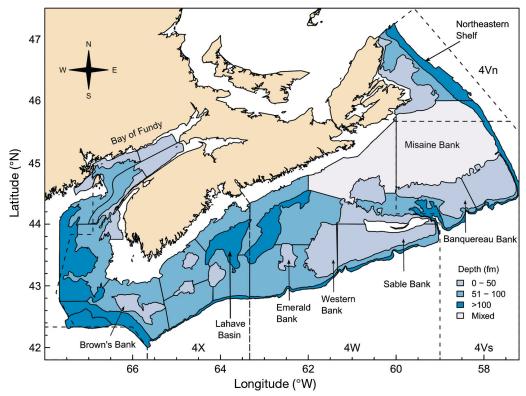
Fig. 1. Research vessel survey strata (stratified random design, 48 strata) and Northwest Atlantic Fisheries Organization (NAFO) divisions for the Scotian Shelf. Dashed lines are NAFO divisions, solid lines are the strata boundaries. Depths are given in fathoms (fm), 1 fathom = 1.8288 m

sity using research vessel trawl survey data (Scott 1976, Mahon & Smith 1989, Frank & Shackell 2001, Shackell & Frank 2003). The invertebrate data have not previously been included in these analyses as they were not consistently recorded in the research vessel sampling program prior to the late 1990s. To complement these studies and build upon our existing knowledge (Breeze 2004, Zwanenburg et al. 2006, DFO 2007, Doherty & Horsman 2007), we evaluated how much additional information on species richness is provided by fish stomach content data and how this could contribute to the definition of EBSAs. Initially we compared the size distributions of samples collected by trawls and from stomachs. Next we explored how these additional data changed our view of finfish and invertebrate species richness both spatially and with regard to the relationship between species richness and environmental variables. We compared species' frequency of occurrence from trawl and stomach data to further our understanding of the dynamics and distribution for poorly understood species. Finally, we compared the results identifying areas of interest from survey data, stomach data, and the combined data.

MATERIALS AND METHODS

Data sources

Data from trawl surveys. Research vessel (RV) surveys of the Scotian Shelf have been conducted by the DFO annually each summer since 1970. These bottom trawl surveys use a stratified random design, with the 48 strata defined by depth range and geographic locations (for further details see Doubleday 1981; our Fig. 1). In addition to the net sampling at each station, CTD casts are performed to collect temperature and salinity profiles. The catch sampling protocols changed in the late 1990s with an extension in focus from commercially important finfish species to broader ecosystem monitoring, including the sampling of macroinvertebrates (Tremblay et al. 2007). In order to encompass this richer data source, the data used in the present analysis were limited to the present time period (1999 to 2008). During this time period, protocols included identification of all species captured, quantitative assessment of total numbers and/or total weight for all species, and detailed information on length and weight for all species of finfish, squids, crabs, and scallops.

Data from the stomach samples. Stomach contents were collected from a length-stratified sample of finfish, and prey were quantified by weight and number. Where possible, prey items were identified to species level; however, due to varying levels of digestion, prey were often identified to genus or family levels. For this analysis, we included some family groups where individual species are infrequently identified (for further details see Cook & Bundy 2010).

Data inventory. Species richness sampled by the trawl and stomach surveys was first compared using a simple count of species by year and sampling methodology for the following categories: small finfish (<15 cm), total finfish, invertebrates, and total species. Length measurements were available for most species, and any gaps were assumed to follow the same distribution as the measured species. American lobster measurements were based on carapace length (CL) which were converted to total length (TL, cm) using $TL = (CL - 8.68) \times 0.3954^{-1}$ (Wilder 1953). Decapod shrimps were not measured but can constitute a significant proportion of the catch. To include these data, shrimp lengths were randomly sampled from a normal distribution of mean (± SD) of 12 (± 2) cm to represent the likely size range (D. Hardie pers. comm.), with the number of samples based on the numbers of individuals captured in the trawl. To determine whether the 2 methodologies sampled different finfish length groups or different invertebrate species, the frequency of occurrence by finfish length group within species, and the frequency of individual invertebrate species occurrence in the 2 sampling methodologies were compared using *t*-tests.

Species richness estimation and extrapolation. We extrapolated species richness estimates using the Chao2 estimator (Chao 1984, Colwell & Coddington 1994) for trawl data, stomach content data, and the combination of the 2 data sources for the different species groups defined above. Additionally, species accumulation curves were generated for finfish grouped by species found within the length intervals (TL) from 1–5, 6–15, 16–25, and >25 cm. These curves were generated using each survey set as a base unit (i.e. for the trawl data, all species observed in 1 set were included, and for the stomach data, all prey species observed across all stomachs sampled in 1 set were included). The adequacy of sampling was determined by calculating the percent difference between the number of observed species and the number extrapolated. Species found in both trawl and stomach data were assigned to the trawl data pool in order to focus on the contribution of the fish food habits data to the overall picture of species richness.

Spatial patterns in species richness and influence of environmental factors

Mapping richness. Prior to mapping the data, survey sets were gridded by location using a grid size of 272 km², which is a small enough scale to allow for regional patterns to be explored, but still allows for the grouping of proximate tows. Within each grid, species richness was measured as the total number of species identified in each sampling block from trawl data, stomach data, and the 2 sources combined. This gridding method assumes that the actual number of species present may not be represented within a single sample, and multiple samples within a grid will improve the species richness estimates provided that there is limited species turnover among samples. Given the short time period of the data used, these assumptions can be considered valid (Shackell & Frank 2003). Richness was calculated for total finfish, small finfish, invertebrates, and the total species.

In order to incorporate spatial autocorrelation in the analyses of regional patterns, the distance between grids was calculated by measuring the shortest distance between the centroids of each block using queen contiguity of the nearest neighbors using spatgraphs (Rajala 2011), spatstat (Baddeley & Turner 2005), and fossil (Vavrek 2010) in R version 2.13 (R Development Core Team 2011). Bottom temperature (hereafter 'temperature') and depth were estimated from RV survey data for each station for each grid by calculating the mean of observed tows.

The model. The spatial patterns in species richness of total finfish, small finfish, invertebrates, and total species were visualized as the species richness present in each map grid. Since sampling intensity is not uniform across the area, and higher sampling intensity will generally lead to higher number of species discovered, differences in sampling intensity were taken into account using a generalized additive modeling (GAM) approach. The predictor variable, sampling intensity, was measured as the number of sets within a grid, which provides a common metric for the trawl and stomach data. The response variable, species richness, was defined as above and was treated as a Poisson process (count data). A color scale was based on the residuals from the model fits. Positive residuals suggest that more species were identified than predicted based on the level of effort. All GAMs were fitted using the R package mgcv (Wood 2006).

Influence of environmental factors and the estimation of spatial patterns in species richness. The potential relationship between environmental variables, temperature and depth, and species richness

of total finfish, small finfish, invertebrates, and total species from the 2 methodologies was explored with GAMs. Similar to the mapping processes above, a Poisson distribution of species richness and sample intensity were included in the model. Model terms were removed if not significant (p > 0.05) and analyses were rerun. If the approximate degrees of freedom for any smoothed term were near 1, analyses were rerun treating that parameter as a linear predictor (Zuur et al. 2009). After fitting the model with only significant terms, residuals were tested for spatial autocorrelation through semivariograms and calculation of Moran's I (Gittleman & Kot 1990). Spatial autocorrelation was included in the model if Moran's I was significant (p < 0.05). The appropriate spatial autocorrelation matrix was chosen based on the shape of the smoothed semivariogram relationship (Legendre & Legendre 1998) and was included in the model via the covariance matrix.

Species-specific analysis. The data for sand lance *Ammodytes* spp., a key forage taxon on the eastern Scotian Shelf, occurred in high enough frequency in both trawl and stomach samples to enable analyses to explore what additional information about sand lance distribution and species–habitat associations could be learned from the stomach survey. For the calculation of catch rates and species–habitat associations, it was necessary to develop a common measure of abundance prior to comparing and combining the trawl and stomach data, since sampling efficiencies of the trawl net and stomachs differ. We do not have estimates of the selectivity of predators for their prey, nor of the vulnerability of prey to predators, but there are estimates of the catchability of fish to trawl survey gear for the Scotian Shelf (Harley & Myers 2001). We thus corrected for the catchability of predators by the trawl survey gear and scaled up the estimates of sand lance accordingly. Briefly, we used a catchability correction and length-based estimates of consumption to account for ontogenetic shift in diet (Link & Garrison 2002) and the differential catchability of predators. For each predator (p_i) and length (l_j) group of species (k) we calculated the number of individual sand lance (n_{ijk}) consumed divided by the number of examined stomachs (w_{ij}). The resultant mean number consumed was then scaled up by the number of predators of the specific length group captured in the trawl (c_{ij}) which was adjusted for the relative catchability of that length group (q_{ij}). Length-corrected catchability was estimated using the logistic model and species or functional group parameter estimates (α_i, β_i, γ_i) provided by Harley & Myers (2001):

$$T_k = \sum_{i=1}^{p} \sum_{j=1}^{l} \left(\frac{\sum n_{ijk}}{w_{ij}} \times \frac{c_{ij}}{q_{ij}} \right)$$

where (1)

$$q_{ij} = \gamma_i \frac{e^{(\alpha_i + \beta_i l_j)}}{1 + e^{(\alpha_i + \beta_i l_j)}}$$

Distribution. One commonly calculated metric used to examine species dynamics is the design weighted area occupied (DWAO) by species. This index shows the change in distribution and concentration of the species over time and gives an indication of population abundance changes and movements or expansions. DWAO was calculated following the methods of Smedbol et al. (2002).

Species–habitat associations. The relationship between sand lance distribution and the habitat variables temperature and depth was explored using cumulative distribution functions (Perry & Smith 1994) comparing available habitat, $f(t)$, with habitat occupied, $g(t)$.

Randomization tests were used to test the significance of habitat associations. The test statistic, L, is the maximum absolute difference between the $f(t)$ and $g(t)$ curves. Statistical significance of L was determined by its comparison with the distribution of values from 2999 random perturbations of the data (3000 repetitions, including L; Perry & Smith 1994).

RESULTS

Species inventories, size distribution, richness, and frequency of occurrence

The number of species identified increased across the time series for both the trawl data and the stomach content data despite similar numbers of trawl sets over time and decreasing number of stomach samples (Table 1). The increase in species richness in the trawl survey, mainly due to the increase in the number of invertebrates identified, increased from 36 in 1999 to 106 in 2007. This was a direct result of DFO starting to systematically record invertebrates in annual ecosystem trawl surveys of the Scotian Shelf in 1999 (Tremblay et al. 2007). There were on average twice as many species sampled in the trawl survey than the stomach program, which may be a consequence of digestion and resolution of prey identification in the latter, rather than actual species presence.

Table 1. Number of total finfish, small finfish (<15 cm), invertebrates, and total no. of species collected in trawl surveys (with no. of trawl sets) and stomach contents analyses (with no. of stomachs analysed)

Year	Trawls					Stomachs				
	Total finfish	Small finfish	Inverte-brates	Total	N sets	Total finfish	Small finfish	Inverte-brates	Total	N stomachs
1999	79	61	36	115	191	25	25	44	69	10352
2000	80	57	30	112	213	20	19	36	56	9546
2001	73	50	22	95	201	23	23	24	47	5055
2002	84	61	46	131	208	17	16	20	37	2472
2003	84	60	37	121	216	–	–	–	–	–
2004	73	53	32	105	188	–	–	–	–	–
2005	94	69	66	162	397	27	21	60	87	1824
2006	83	56	56	139	210	21	19	54	75	1210
2007	82	56	106	189	177	22	19	58	80	3526
2008	83	61	105	189	165	28	22	65	93	3500

In total, 330 species were observed in the trawl and stomach surveys from 1998 to 2008. Many of these species were observed in the trawl survey (294), but when all species and size groups were considered, the stomach data contributed an extra 11% (36) of species to the species inventory for the Scotian Shelf (Table 2). These additional species were entirely composed of invertebrates, which added an additional 19% to the total invertebrate count. The stomach data did not provide any additional finfish species, but did add information on the small size classes, in particular the 1–5 cm group, where an additional 10% (5) of species were observed (Table 2).
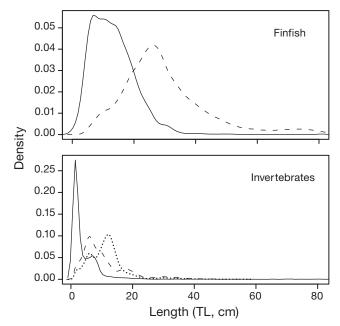
The total number of species predicted from the Chao2 estimator from both the trawl and stomach data was 401 from 1998 to 2008, an increase of 22% from the observed values (Table 2). Similar to the observed species richness, the total estimate of extrapolated species richness derived from the trawl sample was double that found in the stomachs (359 compared to 172). The Chao2 predicted species richness showed an overall increase of 22% when compared to the trawl survey and 17% when compared to the stomach survey. There was substantial variability in the difference between observed species richness and predicted species richness with data source, groups (fish or invertebrate), and finfish sizes (Table 2). Small fish were the most poorly sampled group by both methods, although the largest difference (95%) occurred for small fish (1–5 cm) estimated from the trawl data. In most cases, the percent change for the trawl and stomach data combined was lower than or equivalent to that from the trawl data alone, showing the value of incorporating the stomach data. The 2 species groups that benefited the most from incorporating the stomach data were the invertebrate group and the smallest finfish group,

where the percent change dropped from 17 to 15% and 95 to 37%, respectively (Table 2).

This result is confirmed in a comparison of the size distribution of the samples from the trawl and stomach data (Fig. 2): the stomach data consisted of a greater proportion of small finfish and smaller invertebrates than the trawl data. The modal size of finfish was 26 cm in the trawl survey and 6 cm in the stomach data; the modal size of invertebrates was 6 cm in the trawl survey and 1 cm in the stomach survey.

Table 2. Number of species observed, Chao2-extrapolated estimates ± SD of species richness, percent contribution of the 2 data sources (stomach contents analysis and trawl surveys) to the overall species richness patterns, and difference (%) between observed and extrapolated estimates

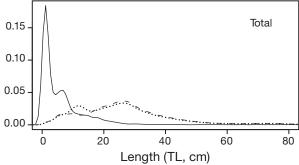|		Actual species	Chao2	Contrib. (%)	Diff. (%)
All species	Stomachs	147	172 ± 5.9	11	17
	Trawls	294	359 ± 9.8	89	22
	Combined	330	401 ± 10.3		22
Total finfish	Stomachs	47	83 ± 11.6	0	77
	Trawls	142	190 ± 11.8	100	34
	Combined	142	188 ± 10.8		32
Finfish 1–5 cm	Stomachs	19	31.5 ± 5.9	10	66
	Trawls	45	87.7 ± 14.5	90	95
	Combined	50	68.3 ± 6		37
Finfish 6–15 cm	Stomachs	35	58 ± 9.2	1	66
	Trawls	105	127.8 ± 5.6	99	22
	Combined	106	130.3 ± 6.2		23
Finfish 16–25 cm	Stomachs	26	29.5 ± 2.5	1	13
	Trawls	84	109 ± 7.3	99	30
	Combined	85	112.6 ± 7.8		32
Finfish >25 cm	Stomachs	22	24.6 ± 2.1	0	12
	Trawls	74	106 ± 10.6	100	43
	Combined	74	106 ± 10.6		43
Inverte-brates	Stomachs	100	109 ± 3.1	19	9
	Trawls	152	178 ± 5.6	81	17
	Combined	188	217 ± 6.2		15

Fig. 2. Length-frequency distributions for finfish, invertebrates, and their combination, sampled from stomach contents and trawl surveys. Long dashed line = trawl data, solid black line = stomach data, dotted line = trawl data including shrimp. Shrimp are not generally measured on the survey but were included in this distribution assuming a measured sample size of 1% of total shrimp catch with lengths drawn from a random normal distribution with mean (± SD) of 12 ± 2 cm

When shrimp were included in the trawl survey data, the modal size of invertebrates increased to 12 cm. When invertebrates and fish were combined, the difference between the modal lengths of the 2 data sources increased (Fig. 2).

Small finfish species from stomach samples had consistently higher frequency of occurrence than those collected in the trawl samples (Fig. 3). All finfish species captured at size 0–5 cm occurred more frequently in stomach samples than in the trawl net. For 6–15 cm fish, 44% (8/18) of species were found in higher proportions in stomachs.

The 2 types of survey sampled the finfish and invertebrate groups selectively, in terms of species and size. Of the invertebrate species that co-occurred in the trawl and stomach data, mesozooplankton, polychaetes, krill, and gastropod species showed up more frequently in stomach data than in the trawl data, whereas cephalopods, bivalves, crabs, echinoderms, and shrimp species were caught more frequently in the trawls (Fig. 4).

Spatial effects on species richness

The GAMs accounted for a significant proportion of the variability in sampling effort between locations (explaining
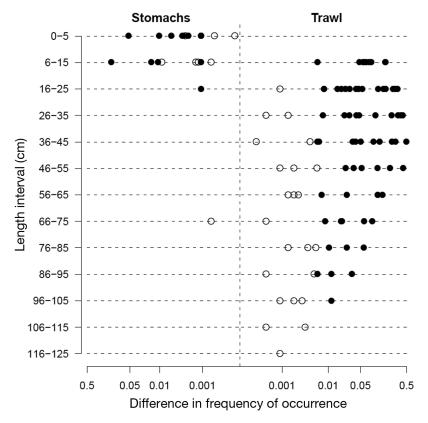

Fig. 3. Difference in frequency of occurrence between stomach content samples and trawl samples for individual finfish species broken down by length intervals (cm). Points to the left of the dashed vertical line represent length intervals of species which occur in greater frequency in stomach contents, whereas those to the right of the dashed line represent length intervals of species with greater frequency in trawls. Filled circles represent statistically significant differences (p < 0.05, t-test)
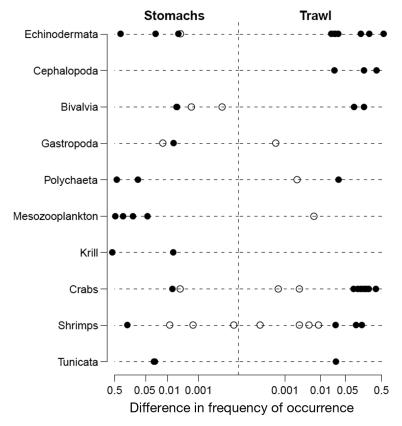
Fig. 4. Difference in frequency of occurrence between stomach content samples and trawl samples for individual invertebrate species grouped taxonomically. Points to the left of the dashed vertical line represent length intervals of species which occur in greater frequency in stomach contents, whereas those to the right of the dashed line represent length intervals of species with greater frequency in trawls. Filled circles represent statistically significant differences ($p < 0.05$, t-test)

between 55 and 75% of deviance) and were thus considered useful for the standardization of the data to a common level of effort. Species richness varied spatially by data source for all species groups examined (Fig. 5). From the trawl data, total finfish species richness was higher across a broader portion of the Scotian Shelf than the small finfish species richness. The highest finfish species richness for both groups was in the Bay of Fundy, Brown's Bank, and on the northeastern shelf (Fig. 5), whereas the lowest finfish species richness was on the western portion of Sable Bank and Banquereau Bank and in the Northwest Atlantic Fisheries Organization (NAFO) Division 4W. Small finfish species richness was similar, but relatively lower in the mouth of the Bay of Fundy and higher on the northeastern shelf and Misaine Bank. Finfish species richness from stomach data was less variable (fewer dark red and dark blue squares in Fig. 5). The distribution of highest species richness of

total finfish and small finfish was similar to that from the trawl data for small finfish, focused on Brown's Bank, the upper part of the Bay of Fundy and, to a lesser extent, the northeastern shelf. In contrast to the trawl data, there was significantly higher finfish species richness in the stomach data in 4W than on the banks in 4Vs (Fig. 5).

The most striking difference between stomach data and the trawl data was for invertebrate species richness. The trawl survey data indicated much higher invertebrate species richness on the eastern Scotian Shelf than the western Scotian Shelf, which can largely be attributed to the increased number of shrimp and bivalve species identified in this region. In contrast, the invertebrate species richness obtained from the stomach survey was more spatially even, with the highest species richness primarily on Brown's Bank and the Bay of Fundy. The combined invertebrate species richness revealed the same higher species richness from trawl data on the northeastern Scotian Shelf, but dispersed the gradient across the shelf with the addition of the stomach data. The central portion of 4W remained the region of lowest invertebrate species richness.

Overall, total species richness varied spatially and between data sources. In the trawl data, highest species richness was observed on the northeastern shelf and in the Bay of Fundy, whereas the highest species richness in the stomach data was found on Brown's Bank, the Bay of Fundy, and 4W (Fig. 5). However, the stomach data were more homogeneous than the trawl survey data. The combined data showed a pattern of high species richness in the east and in the west with an area of low species richness in the central 4W region. There was less evidence of this low species richness area in the stomach data.

Both temperature and depth significantly affected species richness across the Scotian Shelf (Table 3), although in most cases, the proportion of variation explained was small. Species richness relationships were mostly non-linear with depth and linear with temperature (Fig. 6). For depth, both the small and total finfish groups showed similar non-linear patterns for the trawl survey data with the highest species richness at depths of 90 to 140 m, lowest species richness at the shallowest depths, and marginal decreases or plateaus at depths beyond 140 m. Finfish species richness from the stomach data was not significantly affected by depth ($p > 0.1$; data not
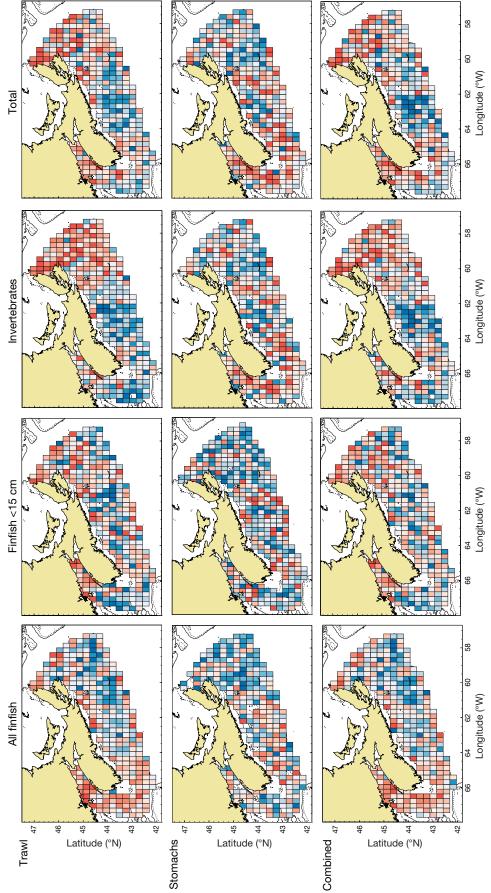
Fig. 5. Species richness across the Scotian Shelf for all finfish, small finfish (TL <15 cm), invertebrates, and total species for samples taken from the trawl surveys, stomach contents, and their combination. Richness was standardized by the level of effort in each square: the color gradient represents the residuals from each model and ranges from large negative values (blue) to large positive values (red), with white representing residuals near 0

Table 3. Generalized additive model output results for the effect of temperature and depth on finfish, invertebrate, and total species richness across the Scotian Shelf, for each data source (trawl surveys and stomach contents analysis) and sources combined. Parameters were either linear (l) or smooth (s) based on their relationship with response variables. 'Proportion of variance explained' represents the proportion of the overall variance explained by each variable. 'Deviance explained' is the overall proportion of deviance explained by the model. Significant Moran's *I* ($p < 0.05$) indicated the presence of spatial autocorrelation resulting in the model being fitted with appropriate spatial corrections. Non-significant ($p < 0.05$) environmental variables were dropped from the final models and are not presented here. Small finfish: TL < 15 cm

Data source	Richness measure	Parameters (linear or smoothed)	Proportion of variance explained	p	Deviance explained	Moran's *I*	p
Trawls	All finfish	Depth (s) Temperature (l)	0.11 0.01	<0.0001 <0.0001	0.56	−0.04	<0.0001
	Small finfish	Depth (s)	0.02	<0.0001	0.48	−0.017	<0.0001
	Invertebrates	Depth (l) Temperature (l)	0.001 0.17	<0.01 <0.0001	0.57	−0.019	<0.0001
	Total	Depth (s) Temperature (l)	0.03 0.03	<0.0001 <0.0001	0.60	−0.04	<0.0001
Stomachs	All finfish	Temperature (l)	0.02	0.01	0.49	−0.0003	0.84
	Small finfish	Temperature (l)	0.02	0.01	0.49	−0.0003	0.84
	Invertebrates	Depth (s) Temperature (l)	0.07 0.01	<0.0001 0.03	0.67	−0.004	0.27
	Total	Depth (s) Temperature (l)	0.03 0.01	<0.0001 <0.001	0.72	−0.004	0.5
Combined	All finfish	Depth (s) Temperature (l)	0.07 0.019	<0.0001 0.0002	0.56	−0.02	<0.0001
	Small finfish	Depth (s)	0.04	<0.0001	0.49	−0.007	0.03
	Invertebrates	Depth (s) Temperature (s)	0.04 0.07	<0.0001 <0.0001	0.67	−0.01	<0.0001
	Total	Depth (s) Temperature (l)	0.03 0.03	<0.0001 <0.0001	0.67	−0.03	<0.0001

shown). There was a negative linear relationship between trawl data invertebrate species richness and depth, whereas both the stomach data and the combined data showed clear non-linear patterns with depth, with the highest species richness in the shallowest waters down to 80 m, decreasing species richness down to 130 m, and plateauing or marginally increasing to 210 m (Fig. 6). Note that the uncertainty associated with these estimates increased with increasing depth due to decreased sample size. Despite the difference in shape, the trawl and stomach data model fits were essentially linear to a depth of around 240 m. Total species richness for both data sources and the combined data showed the highest levels at 90 to 140 m, and decreased at shallower and deeper depths. For depth, all model fits explained less than 5% of the variation, with the exception of all finfish in the trawl survey (11%), invertebrates in the stomach data (7%), and all finfish in the combined data set (7%) (Table 3).

We found positive and negative linear relationships between species richness and temperature: they were positive for all species groupings sampled in the stomach data, and for the total finfish group in the trawl survey data. However, we found a strong negative linear relationship between trawl survey invertebrates and temperature. This relationship resulted in negative relationships with temperature for the total species richness from the trawl data, the total invertebrate species richness, and the combined data total species richness (Fig. 5, Table 3). Furthermore, this negative relationship between trawl data and invertebrates explained more than 17% of the variation in the data; all other model fits explained less than 5% of the variation, with the exception of invertebrates in the combined data (7%) (Table 3). There was no significant relationship between small finfish and temperature for the trawl data and the combined data.

The deviance explained by the model fits (variance explained by the fit of the model to depth, temperature, and effort correction) varied from 48 to 72%, indicating that the effort correction contributes more than depth or temperature to the model fit. Interest-
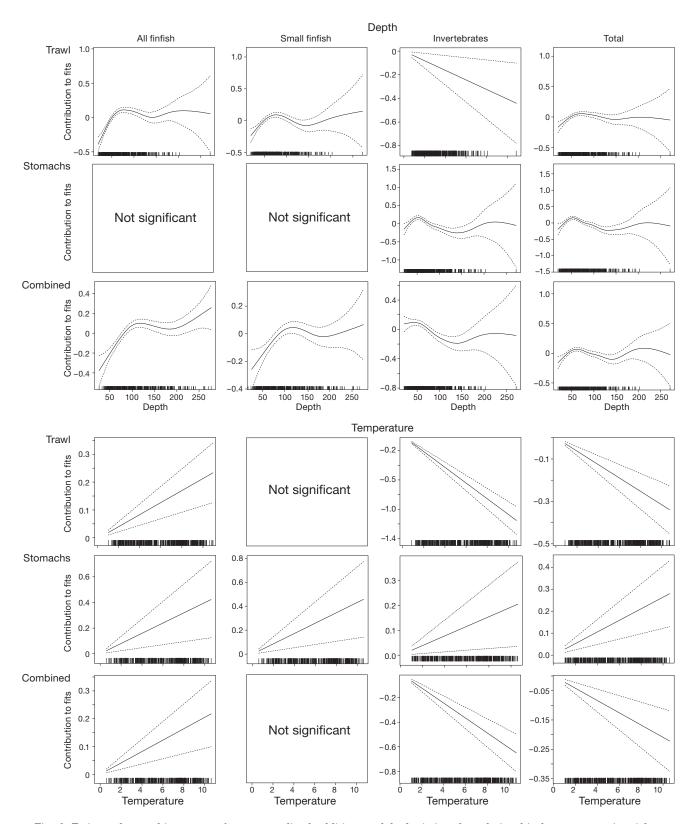
Fig. 6. Estimated smoothing curves from generalized additive models depicting the relationship between species richness from the trawl samples, stomach content samples, and their combination with the environmental variables temperature and depth. The *x*-axes represent the explanatory variables, i.e. either temperature or depth. The *y*-axes represent the contribution of the smoother to the scaled and logit-transformed species richness values. Dotted lines represent confidence bounds around the smoothed curves. Rug plots on the *x*-axis indicate the intensity of observations

ingly, the trawl data showed strong significant spatial patterns in the residuals whereas the stomach data did not show any patterning as indicated by Moran's *I* and corresponding p values (Table 3). This can be seen in the spatial patterns observed in Fig. 5 as there are much stronger patterns of high and low species richness levels in the trawl data compared to the stomach data.

In general, the integration of stomach data with the trawl data did not change the overall relationship between species richness and temperature despite showing different patterns when considered separately. However, the stomach data did influence the relationship between species richness and depth: the combined data for the relationship between invertebrates and depth was non-linear and clearly more
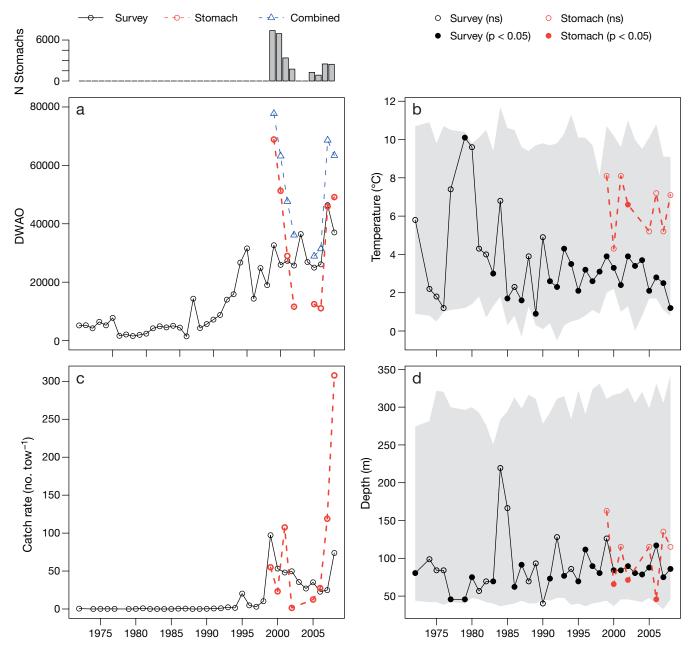

Fig. 7. *Ammodytes* spp. Left panels represent (a) design weighted area of occupancy (DWAO) and (b) catch rate of sand lance from trawl survey data, stomach content data, and the combined data. Barplots above indicate the number of predator stomachs examined for each year. (c,d) Right panels represent habitat preferences from trawl survey and stomach content data, filled symbols represent statistically significant associations (p < 0.05). Shaded area in right panel represents the 95% range of habitat sampled

influenced by the stomach data (Fig. 6). Furthermore, when integrated with the trawl survey data, the stomach data exerted some influence on the depth of maximum species richness for 'all finfish' and 'small finfish,' shifting the maximum to a greater depth. This was in part due to the strength of relationships in the trawl data set as well as the larger number of species identified.

Sand lance (*Ammodytes* spp.)

Based on the trawl survey data, the abundance and the DWAO of sand lance have increased over the past 20 to 25 yr (Fig. 7). Thus in addition to an overall increase in abundance, the area occupied by sand lance has steadily increased since the mid-1990s. The stomach data only date from 1998, but in general, estimates of sand lance abundance and DWAO from the stomach data were consistent with the trawl survey estimates. For each index, the estimates that were higher than the trawl estimates were for the years with higher numbers of stomachs sampled, suggesting there may be a lower limit to the number of stomach samples required to depict these patterns.

Habitat preference data indicated that sand lance sampled by the trawl data preferred temperatures between 2 and 4°C and depths between 50 and 90 m, with means of 2.9°C and 90 m, whereas sand lance sampled by the stomach contents had a higher temperature preference between 6 and 8°C, but a similar depth preference of between 70 and 100 m with means of 6.5°C and 91 m (Fig. 7). For both depth and temperature, the stomach data were more variable than the trawl data, and for temperature, only 1 stomach data point was significant, underscoring the uncertainty of these observations.

DISCUSSION

Value of integrating food habits and trawl surveys

Adoption of an ecosystem approach to ocean management requires a more holistic view and assessment of the ocean's biota. Although used widely, traditional groundfish trawl surveys were not designed for full ecosystem assessments (Jouffre et al. 2010) and only provide measures of abundance for a subset, or slice, of the ecosystem. Here, for the first time, food habits data collected from a trawl survey were integrated with the original trawl data to improve estimates of species richness, distribution, and habi-

tat associations with the objective of providing additional information for an EAM. Initiatives occurring in Canada and globally under an EAM include spatial approaches such as EBSAs (DFO 2004, CBD 2008) and marine protected areas (MPAs, DFO 2005). Such spatial approaches benefit from assessments of species richness, distribution, and habitat associations. For example, specific criteria have been adopted for the identification of EBSAs including uniqueness, aggregation, and life history consequences (DFO 2004); the results presented here can enrich this process. By integrating the food habits data, we have shown that (1) a significant proportion of new species was included in the richness estimations, represented by small invertebrates; (2) the representation of small fish and invertebrates improved, enabling a new, better informed view of their distribution; and (3) food habits data can add information about individual species.

Overall patterns

The spatial analysis of finfish species richness from the trawl survey data confirms results from previous studies that explored the spatial variability in finfish species richness on the Scotian Shelf (Scott 1976, Mahon & Smith 1989, Brown et al. 1996, Shackell & Frank 2003). Using the trawl survey data from 1970 to 2000, Shackell & Frank (2003) identified several areas of high species richness including the Bay of Fundy, Browns Bank, the slopes, Western Bank, and the northeastern shelf. That the results presented here also led to the identification of these areas supports Shackell & Frank's (2003) conclusion that the species composition of the Scotian Shelf has been relatively constant since 1974. We add that the spatial distribution of these species has also been relatively constant since 2000.

To this picture, we added the invertebrates from the trawl survey data and the fish and invertebrates from the food habits data. The overall picture of species richness, combining trawl and stomach content data, finfish, and invertebrates, still largely conforms to the picture described by Shackell & Frank (2003). However, our results indicate that there are both subpatterns within this overall pattern and that there is more to the story. Invertebrate species richness was strongly divided in the trawl survey between the western and eastern Scotian Shelf, where richness was much higher than in the west. In contrast, the stomach data exhibited a pattern where the invertebrate species richness was higher in the west and

Bay of Fundy, and to some extent in the middle of the shelf (4W). Another sub-pattern can be seen for the small fish from the stomach data which occupy more of the central shelf and Western and Sable Bank area than fish from the trawl survey. This pattern is consistent with the larval finfish diversity pattern which was shown to be highest in the same area (Shackell & Frank 2000). Furthermore, these combined results provide evidence to suggest that Western and Sable Bank are important nursery areas for larval and early juvenile finfish on the Scotian Shelf.

The pattern described by Shackell & Frank (2003) and by the finfish trawl survey data presented here does not tell the whole story. Our results also indicate that the species richness in the east extends over the Misaine Bank, due to the addition of the stomach and the trawl survey invertebrate data. Shackell & Frank (2003) also did not highlight the Western Bank as a high-diversity area. Furthermore, when decomposed into invertebrate and small fish groups, the stomach data indicated higher diversity in the middle area of the Scotian Shelf (NAFO Division 4W). The spatial pattern of finfish from the stomach data was largely determined by small fish, which were more evenly spread across the shelf, indicating likely spatial differences between the distribution of large and small fish. In addition, these results indicate that there are small fish in the middle of the Scotian Shelf (NAFO Division 4WX), in areas where they are not captured by the trawl survey. A high diversity of invertebrates was also observed in this area, and since the stomach data revealed invertebrate species not sampled by the trawl data, this may represent a significant gap in our picture of species richness on the Scotian Shelf. All data sources indicate a lack of species richness in La Have and Emerald Basins, areas greater than 200 m depth on the shelf.

Habitat variables such as temperature and depth did not appear to have strong relationships with the spatial patterns in species richness, with a few exceptions. The strongest relationship was the negative linear relationship between invertebrate richness and temperature from the trawl survey. According to metabolic theory, species richness should increase with temperature (Allen et al. 2006), at least across a large gradient (Roy et al. 1998; marine temperatures of 0 to 25°C), as metabolic and hence evolutionary rates are increased at higher temperatures in ectotherms (Gillooly et al. 2005). At local scales, many other processes may influence this relationship. Several of the invertebrate species observed on the eastern Scotian Shelf are coldwater species such as snow crab *Choinectes opilio* and shrimps (*Pandalus*

borealis, P. montagui) that prefer colder habitats. Thermal thresholds will decrease the range available for species movements; e.g. for snow crab, temperature limits available habitat, such that much of the western Scotian Shelf has temperatures above optimal (Tremblay 1997). The eastern Scotian Shelf has been subject to severe disruption and regime change (Bundy & Fanning 2005, Frank et al. 2005), resulting in a switch from a gadid-dominated system to a largely invertebrate-dominated system (Bundy 2005, Choi et al. 2005). This switch has likely facilitated an increase in invertebrate species richness in the eastern shelf area.

The opposite, positive relationship between stomach-sampled invertebrates and temperature is related to the size composition of the catch: fish stomachs collect small invertebrate species (or stages) at greater frequencies than the trawl net. Thus the positive relationship with temperature is likely due to the different physiological requirements of small-bodied and pelagic invertebrate species, as metabolic rates are higher for small individuals, suggesting that warmer waters are more conducive to growth, production, and species development and evolution will be faster (Gillooly et al. 2001).

There was some relationship between finfish species richness and depth, but species richness of small finfish had no strong relationships with depth or temperature. This is in some contrast with previous results, which indicate that areas of highest finfish biodiversity on the Scotian Shelf are related to environmental attributes such as warm bottom water temperatures and transitional or high energy zones (Mahon & Smith 1989). However, depth is correlated with a number of variables such as substrate type, water temperature, light levels, and other properties on the Scotian Shelf (Mahon & Smith 1989), so the relationship between this broad group of finfish and the environment is likely complex, and this more integrative habitat variable may capture more of this complexity than temperature alone. It is possible that the distribution of species richness of fish on the Scotian Shelf is more affected by other physical features such as transitional or high-energy zones. Within the Bay of Fundy, a high-energy area, the increased species richness may be attributed to the incidence of anadromous fish species intercepted, as there are strong migration patterns around the of the Bay of Fundy through the summer months when the survey occurs (Dadswell et al. 1987). The slope waters are another high-energy zone where there is a higher incidence of deepwater fish in the catch: Themelis (1996) reported 39% more finfish species on the shelf

slope than had been previously reported on the standard surveys. Again, the northeast shelf is strongly influenced by the cape north front and the Cabot Strait front from the southern Gulf of Saint Lawrence which influences oceanography features and also causes species movements between regions and thus increased richness estimates (Stobo & Fowler 2006, Belkin et al. 2009).

Spatial planning, MPAs, and EBSAs

Including small fish and invertebrates from the stomach data enhanced our understanding of their distribution, highlighting the importance of the central area of the Scotian Shelf for small fish, and the importance of the western Scotian Shelf for invertebrates. These additional layers of information could be used in the types of GIS analysis used to define vulnerable marine ecosystems, EBSAs, and MPAs (Palumbi et al. 2003, Friedlander et al. 2007, Zwanenburg et al. 2010). For example, 1 of the 3 main criteria for identifying EBSAs is 'fitness-consequences' (DFO 2004), which relates to areas important for key life history functions. The presence of areas important for small fish provides essential information for 'fitness-consequences' not heretofore noted in the Maritimes Region EBSA and MPA processes and should be explored in more detail to understand for which species these areas are important and why. Similarly, the importance of the western Scotian Shelf for invertebrates should be explored further, as much of the current information on invertebrate richness and assemblages comes from small geographic areas using video, still photographs, and benthic grab samples (Wildish et al. 1989, Kostylev et al. 2001).

Poorly understood species

In addition to their valuable contribution to spatial planning, the stomach data also add information about poorly understood species, such as sand lance, a key forage species on the eastern Scotian Shelf. Prior to the early 1990s, sand lance abundance was low and sporadic, but since the early 1990s, its abundance increased to more than 500 times the abundance in the early 1980s, based on RV survey data. However, there has been debate concerning whether this change is real, or the result of a change of behavior of sand lance resulting in increased catchability (Bundy 2005, McQuinn 2009). Our results provide support for the argument that sand lance abundance

has increased: (1) the DWAO estimate from the stomach data is comparable to the estimates from the RV data, indicating that the area occupied by sand lance has increased, as predicted with increasing abundance (Gaston & Blackburn 1999); (2) sand lance sampled by the RV surveys or in stomachs occurred at similar depths, indicating that the DWAO from the stomachs is representative. This uncertainty about the dynamics and abundance of sand lance and other forage fish on the Scotian Shelf is a key gap to fill in order to improve our understanding of ecosystem structure and functioning.

Practicalities of using stomachs

We have shown above that using fish as samplers gives information on the smaller size classes of biota, which are poorly sampled by trawl survey, and adds to our understanding of species richness across the Scotian Shelf. However, it must also be recognized that this data source has a suite of pros and cons, comparable to that of trawl surveys. The major positive attributes of using fish stomach content data from trawl surveys is that it provides wide spatial coverage, a range of 'gape' sizes (i.e. prey selectivity varies across the range of predators), and the data can be collected and processed (if processed at sea) within 4 to 8 wk. However, there are also other considerations to take into account:

(1) The positional information provided for the prey relates to where the predator was caught by the trawl survey, not where the prey was consumed by the predator. Thus there may be a gap between position of consumption and capture, which can lead to inaccuracies.

(2) At best, trawl surveys estimate the relative biomass of sampled species since catchability is not known for most species, although estimates are available (e.g. Harley & Myers 2001, Brodziak et al. 2004). This uncertainty is compounded when fish are used as additional samplers of the biota since we do not know the catchability of the prey to the predator. Thus in order to estimate the actual abundance of a prey species, estimates of the catchability of the prey to its suite of predators, plus estimates of the catchability of those predators to the trawl net would be required. In the species richness analyses presented here, only presence/absence data were used, so absolute estimates of abundance were not required. However, for the species-specific analyses of abundance and species–habitat associations, we included the catchability of the predators to the trawl survey

gear, but did not incorporate the catchability of the prey to predator in the analysis. Catchability of prey by a predator would be challenging to estimate, as it is the result of a suite of behaviors by predator and prey including foraging behavior, selectivity of the predator, vulnerability of the prey, and prey suitability (Walters & Kitchell 2001, Link 2004a,b, Walters & Martell 2004). However, 1 approach may be to borrow from the functional relationships used to estimate prey consumption in ecosystem models, but there are many different forms of functional relationship (e.g. Koen-Alonso 2007), and uncertainty remains high.

(3) Species identification and taxonomic resolution of prey items is a more challenging task than identifying trawl-captured organisms due to their state of digestion. Current protocols use broad family or generic species groups to account for items which cannot be identified to species. This will invariably decrease the absolute level of species richness from these data. Additionally, rates of digestion vary between prey groups.

Despite these caveats, we have shown that fish stomachs add useful information to our overall understanding, and for many purposes, it is not necessary to estimate the absolute abundance of prey species.

CONCLUSIONS

Taking an ecosystem approach to fisheries and oceans management requires the use of additional data sources to contribute towards creating a more complete picture of the ecosystem. Further, it requires additional methodologies to improve understanding of the structure, functioning, and spatial use of ecosystems. Here we have explored an additional data source and used analytical methods to examine what it can contribute to our understanding of biodiversity, spatial distribution, and the definitions of spatial management tools such as EBSAs on the Scotian Shelf. We have shown that fish food habit data reveal species and size classes not typically observed by trawl data. Further, we have shown that the integration of stomach content data into the information used to define EBSAs can enrich this process and add dimensions that would otherwise be missed. This has important implications for EAM generally since in Canada and elsewhere, we are in the process of defining spatial management tools such as EBSAs, but may not be using all of the resources at our disposal.

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